PREDATOR-UNGULATE RELATIONSHIPS
IN SECOND GROWTH FORESTS
ON VANCOUVER ISLAND

Problem Analysis

INTEGRATED WILDLIFE INTENSIVE FORESTRY RESEARCH

Province of British Columbia

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PREDATOR-UNGULATE RELATIONSHIPS IN SECOND GROWTH FORESTS ON VANCOUVER ISLAND

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Summary

The effects and influences of predation on ungulates are reviewed. Predation is a significant source of mortality and influences the distribution and habitat selection of native ungulates.

Predation effects and influences on Vancouver Island deer and elk are reviewed and contrasted with those of the rest of North America. Predation on deer is particularly severe due to high wolf population densities and the probable additive effects of cougar and bear predation and human deer harvests. Wolves probably influence seasonal movements and habitat selection of deer and elk but the available information is inconclusive.

The potential effects and influences of wolf predation on ungulate populations in second growth forests is high. It presents a major confounding factor in interpreting deer and elk habitat utilization, animal condition, and population parameters. However, it is suggested that wolves should not be viewed as a confounding influence on intensive wildlife intensive forestry management but as an integral component of a managed predator-ungulate-habitat system. Specific problems and unknowns of predation are also identified.

It is recommended that predation studies be implemented immediately. Baseline investigations should be established on all IWIFR second growth study areas and intensive investigations should be initiated in an area where wolf, deer and elk studies can be integrated. An experimental wolf control-removal study should serve as a basis for intensive studies. Logistical and financial constraints indicate that it may be necessary to utilize several study areas to address the various study topics outlined. An alternate research proposal is therefore presented which is feasible but not as satisfactory.

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1 INTRODUCTION

Concern for deer and elk populations in the management of second-growth forests on Vancouver Island has recently increased as more of the Island comes under intensive forestry management. As a result, the Integrated Wildlife Intensive Forestry Research (IWIFR) program, sponsored by the Ministries of Forests and Environment, initiated a five year field research project to investigate how intensive silvicultural practices in second-growth forests can be modified to enhance ungulate populations.

Although the Vancouver Island wolf was considered rare and endangered during the 1950-60's, a substantial increase occurred during the 1970's such that Vancouver Island now supports one of the densest wolf populations in North America (Hebert et al. 1981). Much of northern Vancouver Island is presently exhibiting substantial deer declines, and intense wolf predation appears to be the primary cause (Hebert et al. 1981, Hebert 1981, Jones and Mason 1981, Hatter in prep.). Preliminary wolf-deer studies in mature timber-early regenerating forests have indicated that ungulate responses to intensive silviculture could be drastically masked by intensive predation (Hebert et al. 1981). This has raised a major concern with IWIFR deer and elk researchers who feel that many of the conclusions derived from their research programs could be invalidated by the confounding effect of wolf predation (Janz 1981; Davies, pers. comm.).

The present analysis, funded as part of the IWIFR Program, provides a comprehensive perspective of the predation problem. The primary intents are to identify the unknowns and potential problems of wolf predation on ungulates in second growth forests and to provide recommendations for future research.

2 DEFINITION OF TERMS

Animal condition:

- a measure of the physical health and fitness of an individual.

Compensatory predation:

- the killing of prey animals by predators that would not survive and reproduce in the absence of predation.

"Control-effective" ratio:

- the predator-prey ratio at which predators will effectively control prey numbers (i.e., the number of prey will increase if predation is reduced).

Cutover:

- a logged area still in a seral stage.

Density dependence:

- an inverse relationship between rate of population growth and population density.

Density independence.

- an unpredictable relationship between rate of population growth and population density.

Dispersal:

- movement of individuals into or out of populations.

Escape cover:

- those habitat features, vegetative or topographic that allow a prey animal advantage in moving away from pursuit by predators.

"Effects" of predation:

- the ability of predators to limit or regulate prey numbers, or dampen numerical fluctuations in their prey.

Functional response:

- changes in the number of prey consumed per predator with changes in prey density.

Hiding cover:

- those habitat features, vegetative or topographic, where an animal can rest from predators or hunters, in an unstressed condition.

Home range:

- that area traversed by an animal in its normal activities of food gathering, mating and caring for young, over a specified period of time.

"Influence" of predation:

- the changes in prey behaviour in terms of habitat selection and retention, activity patterns, sociality and wariness as a result of predator activity.

Limiting factor:

- that factor that limits population size, which, when removed results in population growth.

Numerical response:

- changes in the density of predators with changes in prey density.

Population control:

- maintenance of a population through both density dependent and density independent process.

Population regulation:

- maintenance of a population through density dependent processes only.

Predator switching:

- a shift in predator food habits from one prey species to another, usually during or after depletion of the main prey.

Predator interference:

- the ability of one predator species to affect the predatory capabilities of another species and vice versa.

Predisposing factor:

- that factor which renders a prey organism vulnerable to predation and which may be more important as a regulatory mechanism than predation.

Prey vulnerability:

- encompasses all the physical and biological conditions that cause one individual to be preyed on more heavily than another.

Proximate cause of mortality:

- the proximate cause of mortality refers to the immediate agent of mortality (e.g. predation) whereas ultimate causes refer to those factors, usually environmental, which are primarily responsible for deaths (e.g. food shortage, severe weather).

Second growth forest:

- forest growth that has come up naturally after some drastic interference (e.g. wholesale cutting, serious fire or insect attack) with the previous forest crop.

Silvicultural treatments:

- forestry activities undertaken to enhance production of commercially valuable tree species including thinning, silvicultural fertilization, highsite conversion, and commercial thinning.

Spatial heterogeneity:

- the spatial complexity of the environment resulting from a mosiac of habitat types and topographic features.

Surplus killing:

- killing an excess of prey that are not fed upon by the predator, its offpsring or members of the same social unit.

"Threshold of security":

- that density in self-regulating prey species at which individuals become vulnerable to predation because of a lack of secure habitable niches (refuges) in the environment.

3 OBJECTIVES OF THE PROBLEM ANALYSIS

The objectives of the present analysis are to:

1. Review the effects and influences of wolf, cougar, and bear predation on ungulate populations in North America.
2. Review the current effects and influences of wolf predation on ungulate populations from Vancouver Island and compare wolf predation effects on the Island to those of rest of North America.
3. Assess the potential contribution of black bear and cougar predation on Vancouver Island deer and elk.
4. Outline the potential effects and influences of wolf predation on ungulate populations in second growth forests.
5. Recommend studies for future research of predators and predator-prey relationships in second-growth forests.

4 SCOPE OF THE PROBLEM

Initially, the problem analysis was restricted to identifying the effects of wolf predation on deer and elk populations in second growth forests and the potential of intensive silviculture to alter existing inter-specific relationships. However, it was recognized that a full evaluation of predatory effects also requires knowledge of cougar and black bear predation (ESSA 1981). Accordingly, the problem analysis was modified to follow the large mammal systems approach, similar to that employed in Canadian National Parks (Carbyn 1979). A conceptual model of the Vancouver Island predator-ungulate system is shown in Figure 1. The system is broken into two components, the interrelationships between predators, prey and vegetation, and the influence of external factors to the system (i.e., weather, hunting, and forestry).

This analysis is a first attempt to define the problems of predation on deer and elk in second growth forests. Given the many interactions possible at the system level (e.g., predator switching, predator interference, compensatory mortality), it is not presently possible to realistically address all the potential problems. Many conceived problems may be insignificant while others may be identified when more baseline data are available.

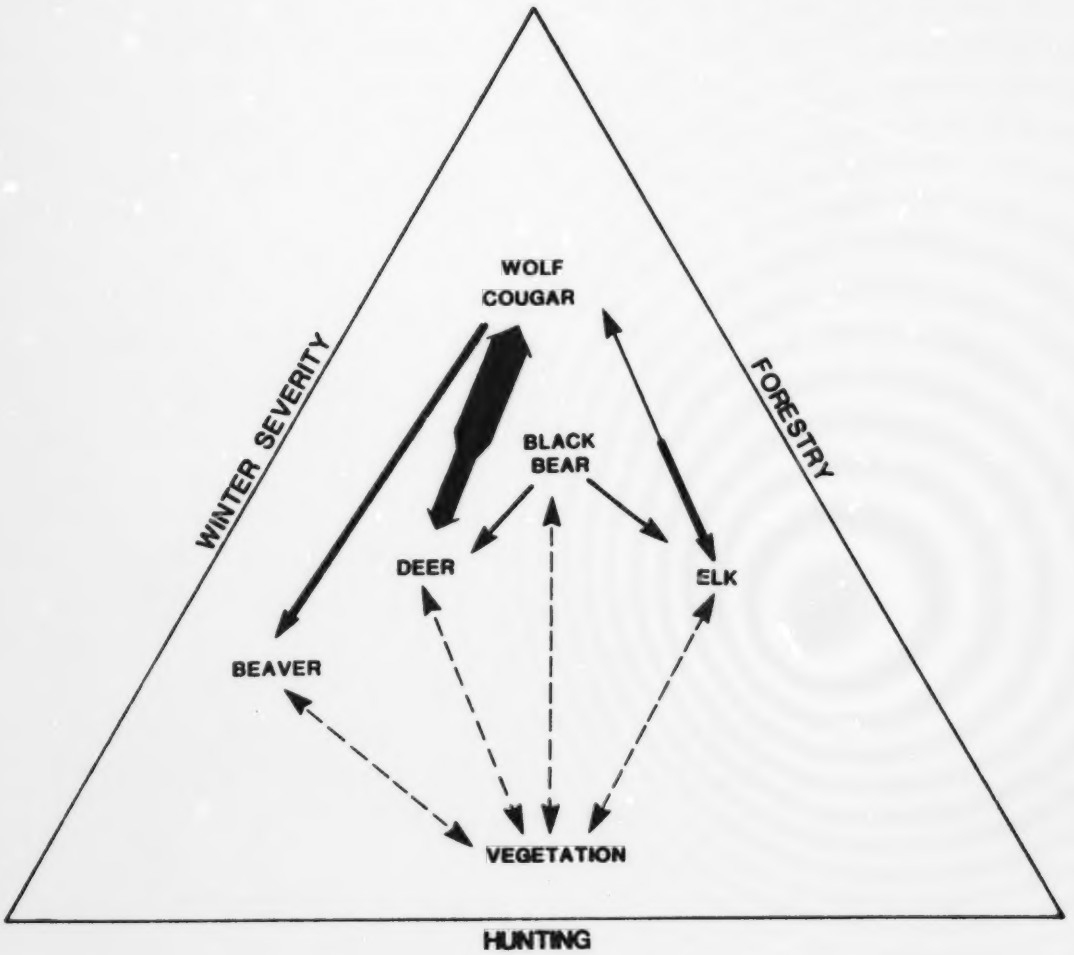

Figure 1. Conceptual model of the predator-ungulate system on Vancouver Island. One-way solid arrows indicate predator-herbivore interactions. Two-way solid arrows imply at least partial regulation between predators and herbivores. The thickness of the arrows indicates the importance of the interaction. Dashed arrows refer to vegetation-herbivore interactions.

5 SCOPE OF PRESENT KNOWLEDGE

5.1 Predator-Prey Relationships - General Theory

The effects of predation on prey density depend on five different variables (Leopold 1933, Holling 1959): (1) density of the prey population (2) density of the predator population (3) characteristics of the prey, e.g., defense or escape capability (4) characteristics of the predator, e.g., food preferences, ability to detect, capture and kill prey, and (5) density and quality of alternate foods available to the predator. It is from the first two variables that the basic components of predation are derived. Holling (1959) referred to these as the "functional response" or change in number of prey consumed per predator, and the "numerical response" or change in density of predators. The other three variables are subsidiary components since they are not essential to describe the fundamental characteristics of predation, although they may have a marked effect on it.

Holling (1959) recognized four types of predation depending on the functional response of the predator, but only types three and four apply to vertebrate predation. Under type three predation, regulation of prey by the predator is considered possible regardless of the predators numerical response. Regulation results whenever a rise in percent predation over some range of prey densities occurs and the effective birth rate of the prey is matched at some density by mortality from predators. Even if a predator cannot regulate the prey population alone, it still may be capable of dampening oscillations. Additional mortality from other predators would enable it to partially regulate the prey. Type four predation is the compensatory mortality of Errington (1946). Predators remove the vulnerable population existing above the "threshold of security" and have little or no impact on the prey population below this threshold. However, Errington assumed prey populations are self-regulating and have refuges to escape predators. Although this may be true for some species, many investigators questioned its applicability to ungulates (e.g. Errington 1963, Pimlott 1967, Bergerud 1971, Keith 1974).

An important consideration in evaluating predator-prey systems is the history of the interacting populations. Knowing this, Hornocker (1976) makes two general statements: (1) the limiting effects of predation tend to be reduced and the regulatory effects increased where the interacting populations have coevolved and they occur in a relatively stable ecosystem and; (2) violent, destabilizing, predator-prey interactions happen frequently when the interaction is of recent origin or when there has been a large scale disturbance to the system, either through natural or man-induced change. Bergerud (1971) also noted the fragile balance between predators and prey on islands where perturbations to relatively simple ecosystems may cause severe predator-prey interactions.

Stabilizing mechanisms in predator-prey systems include prey refuges, an invulnerable class of prey, spatial heterogeneneity, predator switching, and the intrinsic growth rates of the predator and prey species (Murdoch 1969, Murdoch and Oaten 1975, Tanner 1975). Holling (1973) and May (1973, 1976) discuss the more theoretical aspects of resilience and stability in predator-prey systems. Haber et al. (1976) describe the stability properties of a wolf-ungulate system in Alaska.

5.2 Predation on Ungulates - Effects and Influences

Hornocker (1976) emphasized that predators both effect and influence ungulate populations. Three possible effects of predation are: (1) the predator can be anti-regulating, i.e., cause prey populations to be unstable and may drive them to extinction or near extinction, (2) the predator can be regulating or maintaining a "steady state" in prey numbers, or (3) the predator may be non-regulating but still able to reduce rates of population growth and thus dampen numerical fluctuations in prey.

The influences of predation refer to the morphological, physiological, and behavioral responses of prey to predators. Behavioral responses may include changes in habitat selection and retention, activity patterns, sociality and wariness. Both the effects and influences of predation must be recognized

and understood if management of predator-prey systems is to be achieved.

5.2.1 Effects of Predation on Ungulate Populations

Much controversy still exists about the effects of predation on ungulate populations. The discussion here is limited to the effects of wolves, cougars and bears on North American ungulates. Messier (1981) outlined four major hypotheses of population limitation in ungulates and the effects that predators have in each.

In the "food limitation" hypothesis predators influence the rate of increase of ungulate populations, with this rate determined by density-dependent intraspecific food competition (Caughley 1976, McCullough 1979). Predation is mainly compensatory at high prey levels. Field studies of cougars (Hornocker 1970), bears (Longhurst et al. 1952, Swartz and Mitchell 1945), and wolves (Cowan 1947, Thompson 1952, Carbyn 1974) have been ascribed to fit this hypothesis. External factors such as hunting or environmental influences (e.g., severe winters, deteriorating habitat), however, may initiate ungulate declines that predators continue (Shaw 1977, Mech and Karns 1977, Peterson 1977).

The second or "predator control" hypothesis is used by Bergerud (1967, 1974) to explain population control in caribou, although it may be applicable to other species as well (Pimlott 1967, Keith 1974, Bergerud et al. 1981). According to this hypothesis, predation acts as a limiting factor on ungulates at a level much lower than the one dictated by the available food supply. A low equilibrium does exist between predator and prey, but the system is imperfectly density-dependent, and the equilibria are easily upset by extrinsic influences (Bergerud 1980). The predator can trigger ungulate declines if predation on juveniles reduces recruitment below the natural mortality rate of adults. Hunting is an important additive mortality agent. An important distinction between this hypothesis and the "multiple equilibrium" hypothesis outlined below is that predators can halt population growth even at high ungulate densities.

The third or "multiple equilibria" hypothesis states ungulate populations can occupy two stable equilibria separated by a zone of instability (Haber 1977, Haber and Walters 1980). If the population is severly reduced, either through overharvesting or from environmental factors or both, predators can regulate the population at a lower equilibrium level. However, if the population increases beyond the zone of instability, predators will have little effect on numbers. Food supply will constitute the limiting factor and set the upper equilibrium.

The fourth or "environmental limitation" hypothesis considers populations to be controlled by density independent environmental factors such as severe winters (Ransom 1967, Potvin et al. 1978). Density dependent regulation from predation decreases in importance as environmental conditions become more variable. Food competition is not operative and recruitment and adult mortality are influenced primarily by abiotic factors. Predation and hunting can have an accelerating effect on declines triggered by winter severity.

It is significant that hunting is considered a potentially important component in all four hypotheses. Connolly (1978:389) stated "It remains to be shown that ungulate populations can thrive under high rates of harvest in addition to predation by unchecked carnivores."

5.2.1.1 Factors Affecting Predator-Ungulate Systems

The most important factors influencing predation in predator-ungulate systems are predator-prey ratios, prey selection, food consumption, alternate prey, and predator and anti-predator strategies. These are essentially a restatement of Holling's (1959) five factors (see 5.1). Messier (1979) also noted that environmental factors such as snow depth, habitat quality and environmental features must be included since they have a significant effect on the vulnerability of prey and consequently affect the whole predator-prey system. Human exploitation (i.e., hunting, logging) also affects the behaviour of the system and must be recognized (see 5.2.1 and Figure 2).

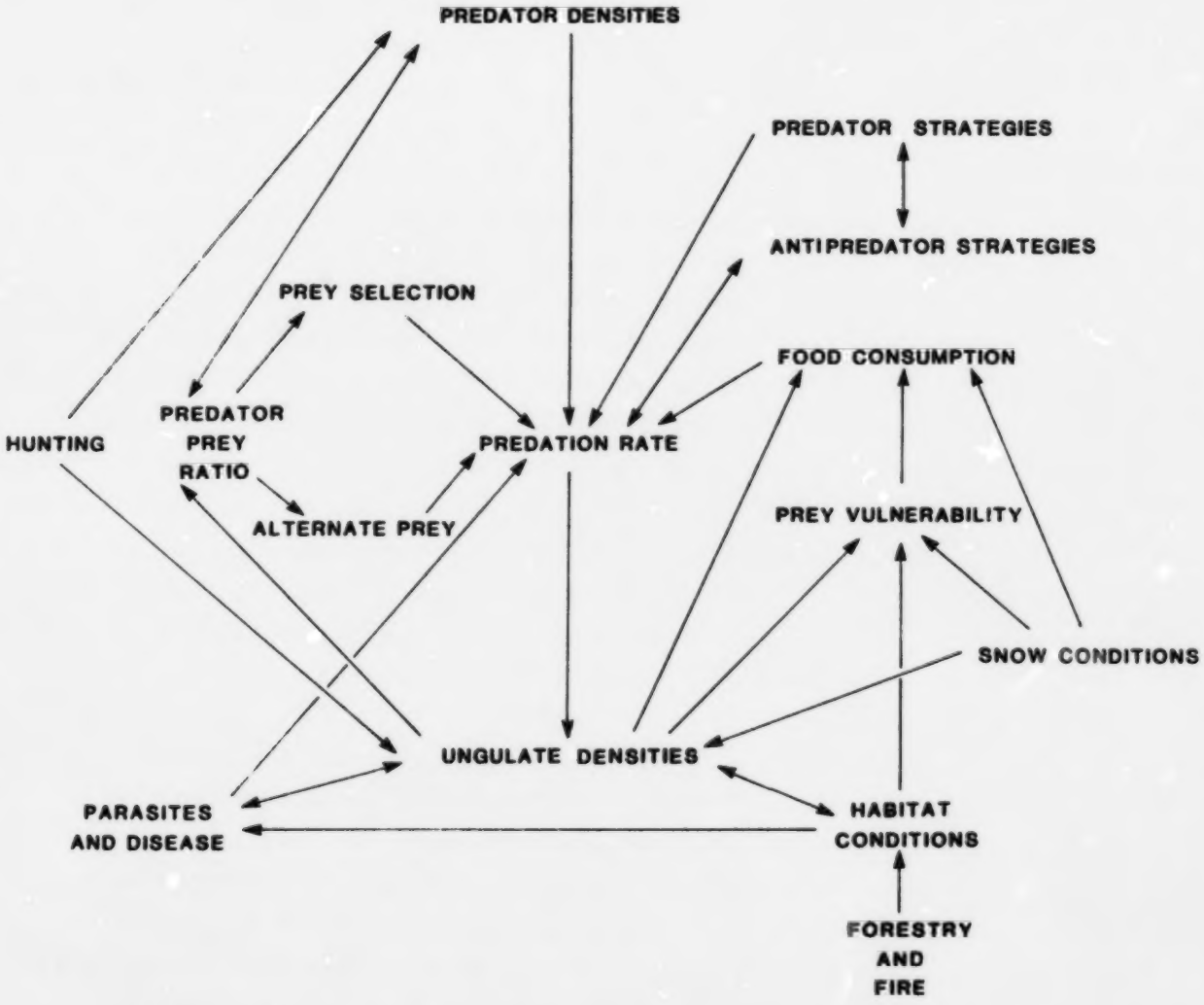

Figure 2. A conceptual model showing factors affecting predator -ungulate systems.

5.2.1.1.1 Predator-Prey Ratio

Keith (1981) in a review of the population dynamics of wolves concluded that "wolf rates of increase are primarily determined by the per capita biomass of their ungulate food supply and that wolf densities in stationary populations are thereby adjusted to total ungulate biomass". Bergerud (1978 b) implied this earlier when he noted that "normal" wolf densities can be established for different wolf/ungulate systems, based on ungulate biomass calculations. Bergerud suggests densities of one wolf/25-50 mi^2 for wolf-caribou-moose systems and one wolf/100-200 mi^2 for wolf-caribou systems. For wolf-deer systems, it is probably about one wolf/10 mi^2 (Pimlott 1967). A cougar-deer-elk system appeared to be stable at one cougar/13 mi^2 (Hornocker 1970).

Predator and ungulate populations, however, are often not stable and wolf-ungulate ratios tend to be dynamic with wolves able to respond rapidly to changes in prey density or vulnerability. Following a series of severe winters and successional maturation of habitat, wolf-moose ratios on Isle Royale changed from 1:80 in 1969 to 1:20 in 1976 as moose delined and wolves increased (Peterson 1976).

Wolf-ungulate ratios often increase during the early stages of an ungulate decline when ungulates become more vulnerable and consistently remain higher than before the prey decline. Messier (1979) concluded this was due to an increase in the percentage of reproductive females at low densities, intensified use of alternate food sources and trespassing into neighboring wolf pack territories.

The predator-prey ratios at which predators effectively control prey numbers are referred to as "control-effective" ratios (Davis et al. 1976). Keith (1981) noted that the ratio for control will depend on: (1) the number of kills per predator annually, (2) the annual rate of increase of the ungulate population, and (3) the proportion of the annual increment to the ungulate population removed by hunting. In the absense of hunting, control-effective ratios have been calculated for wolves to moose at 1:30 (Davis et al. 1976) and

1:50 (Keith 1981), for wolves to caribou at 1:104 (Parker 1972), 1:162 (Davis et al. 1976) and 1:100 (Bergerud 1980) and for wolves to white-tailed deer at 1:100 (Pimlott 1967) and 1:45 (Keith 1981). If hunters remove 50% of the annual increment, control-effective ratios may be halved. Cougars appear to be unable to control deer at ratios of 1:135 to 1:201 (Hornocker 1970). Apparently no attempt has been made to determine bear-ungulate ratios, probably because ungulates comprise a small portion of the diet and bears do not show a numerical response to ungulates.

5.2.1.1.2 Prey selection

Many studies have established that predators select inferior members of prey populations, that is, the young, old and sick. This statement is now considered too simplistic. Selectivity is dependent on the characteristics of predators and prey, and varies according to the density of prey relative to resources and the density of predators relative to the prey population (McCullough 1979, Messier 1979). Thus wolf predation is more specific for younger and older age classes in moose than in deer where hunting success is higher and prey animals are less tested (Mech 1966, Kolenosky 1972). Similarly, selection for older and substandard deer is most prevalent in a high deer population with a low number of wolves but decreases as the deer population declines and the wolf population increases (McCullough 1979). Because of their mode of hunting, cougars show less selection for substandard prey (Hornocker 1970). Predation on juveniles is least compensatory when ungulate populations are below habitat carrying capacity, and most compensatory when ungulates exist at or above carrying capacity (Connolly 1981).

Several investigations have reported that wolves prey disproportionately more on male adult deer (Pimlott et al. 1969, Kolenosky 1972, Mech and Frenzel 1971), and female fawns (Stenlund 1955, Mech and Frenzel 1971, Mech and Karns 1977). Fritts and Mech (1981) suggested that differential predation on adult males resulted from wolf packs killing deer

on the fringe of wintering yards where adult males are more prevalent. Hornocker (1970) believed that bucks and bull elk were more vulnerable to cougars because they winter at higher elevations and are often alone. Thus it appears that selection for sex, as well as age classes, are primarily dependent on the prevailing ecological and behavioural conditions.

5.2.1.1.3 Food consumption and kill rates

Food consumption by predators is calculated by observing the number of kills per predator (kill rate) for a given time and relating this observed rate to food intake (kg/day). Kill rates are dependent on the food requirements of the predator (Mech 1970, Hornocker 1970), size of prey (Keith 1981), vulnerability of prey (Messier 1979), and use of alternate prey (Frenzel 1974). Consumption rates are greatest in winter when snow makes prey more vulnerable and energetic costs of locomotion are highest (Mech 1977a, Haber 1977). Reported winter food consumption for wolves has varied from 1.6 to 10.0 kg/wolf/day (Peterson 1974, Fritts and Mech 1981). Mech (1977a) concluded that more than 3.2 kg/wolf/day is required for successful reproduction. Hornocker (1970) estimated food consumption rates for cougars at 1.8 - 2.7 kg of meat/day. No rates are available for bears, since they usually are not dependent on ungulates as prey.

Surplus killing, where partial or no carcass utilization occurs, has been documented by Pimlott et al. (1969), Mech and Frenzel (1971), Peterson (1974) and Mech and Karns (1977). Habitat and/or climatic predisposing conditions are usually associated with these elevated kill rates. Skoog (pers. comm. to Kruuk 1972) and Miller and Broughton (1974) observed excessive predation on caribou calves on the calving grounds without predisposing conditions. Although the ecological consequence of surplus killing are probably small, they may sometimes become locally and temporarily important (Kruuk 1972, Messier 1979).

5.2.1.1.4 Alternate Prey

Most wolf investigations have revealed that wolves are primarily dependent on one or two types of prey. Increased use of alternate prey species such as beaver or moose usually occurs during or after a depletion of the main prey (Frenzel 1974, Peterson 1977, Voigt et al. 1976). Peterson (1977) and Mech and Karns (1977) concluded that predator switching to alternate prey has the effect of temporarily subsidizing the wolf population and allowing it to remain larger than otherwise possible. This enables wolves to continue exerting unusually high pressure on the reduced main species, probably through increased predation on neonates during summer when they are most vulnerable (Messier 1979, Bergerud 1978b).

Shaw (1977) hypothesized that alternate prey in the form of livestock calves enabled the cougar to maintain a higher density and therefore exert a greater effect on deer than in cases without livestock.

5.2.1.1.5 Environmental Factors

Environmental factors are a critical component in predator-prey systems since environmental attributes are often the ultimate factors involved in predisposing prey to predators (Peek 1980). Mech and Karns (1977) reported that deteriorating habitat and severe winter predisposed deer to heavy predation in Minnesota. Wolfe (1977) concluded that the annual mortality attributable to wolves on Isle Royale varied according to winter severity. Peterson and Allen (1974) showed that deep snow reduced forage availability and lowered moose mobility. This increased malnutrition in calves and consequently their vulnerability to wolf predation in later years.

5.2.1.1.6 Predator Strategies

Stenlund (1955), Kolenosky (1972) Haber (1977) and others have provided observations which suggest that wolves are very effective in locating prey and using hunting strategies that maximize the probability of location. This is probably true for other predators as well.

Predators probably intensify their hunting on local concentrations of prey. This is particularly true for calving

areas where neonates provide an abundant, vulnerable source of prey for wolves and bears (Bergerud and Butler 1978, Miller and Broughton 1974). Haber (1977) reported that one wolf pack in Alaska traditionally denned near a moose calving area and heavily utilized moose calves during the summer months. Wolf packs in Minnesota are frequently found in the vicinity of deer yards in late winter when deer are most concentrated (Fritts and Mech 1981). However, wolf packs did not take advantage of deer and elk concentrations at mineral licks in Jasper National Park, apparently because ungulates were readily available elsewhere (Carbyn 1974).

Both Mech (1977) and Fritts and Mech (1981) reported that more kills were made within the centers of wolf pack territories than along the edges. Miller (1975) also reported that wolf-killed caribou were not randomly distributed and that certain sites must provide wolves with an advantage over their prey. Peterson and Woolington (1981) found most wolf-killed moose on the Kenai Peninsula in old burns, often associated with small stands of timber remaining in the burn.

A strategy of prey exploitation by wolves was documented in Minnesota by Mech (1977). While deer were abundant, wolf packs concentrated their winter kills in separate pockets within 6.4 km of the territory center. Kills tended to be made in new areas each year. The edges of territories or "buffer zones" were avoided by wolves, and Mech (1977b) theorized that deer in buffer zones provide a prey reservoir for dispersal of deer into territory cores. As the deer population declined the distribution of kills became more scattered. After a drastic prey reduction in the territory center, wolves resorted to killing more deer along territory edges and they trespassed into other pack territories. It took five years before deer were numerous enough for wolves to begin killing deer again in their territory cores.

5.2.1.1.7 Anti-Predator Strategies

Hiding, escaping and avoiding predators are important anti-predator strategies, but since they also influence habitat selection, they are discussed in 5.2.3. Other anti-

predator strategies include: (1) freezing behaviour and cryptic colouration of neonates, e.g., deer (Geist 1981); (2) clumping of animals in open habitats, e.g., caribou (Bergerud 1974), sheep (Carbyn 1974) and white-tailed deer (Kramer 1972); (3) solitary behaviour in closed habitats, e.g., deer (Nelson and Mech 1981); (4) synchronization of births, e.g., caribou (Bergerud 1974); (5) protean behaviour, i.e., bewildering, unorientated and erratic displays, e.g., caribou (Murie 1944), stotting in deer (Geist 1981); (6) fending off attackers, e.g., moose (Mech 1966); (7) adopting daily or seasonal activity patterns to reduce predator encounters, e.g., deer fawns (Jackson et al. 1972), and (7) home range fidelity, e.g., deer (Nelson and Mech 1981).

For white-tailed deer, Nelson and Mech (1981) hypothesized that social relationships, migration, yarding and home range location are anti-predator strategies against wolves. In summer, the solitary behavior of does and "freezing" behavior and cryptic coloration of fawns was considered to constitute an optimum defense strategy against predation. In winter, yarding behaviour was thought to provide several significant anti-predator benefits: (1) a system of trails creates escape routes; (2) herding provides greater sensory awareness and makes gregarious animals less vulnerable to predator approach; (3) social grouping may confuse the search image of predators; (4) grouping exposes to wolves the more vulnerable older deer which have already contributed genetically to the population, (5) congregating increases the deer/wolf ratio and decreases relative predation levels, and (6) individual herd members may be able to spend less time alert and more time eating and ruminating. The traditional use of summer ranges and wintering yards on the edges of wolf pack territories also allowed deer to take advantage of the territorial feature of wolf packs.

5.2.2. Influences of Predation on Ungulates

Predators may influence ungulates in several ways. One often cited influence is that predators select substandard prey and thus eliminate or reduce the frequency of inferior genes in the prey population. Mech (1970) used the term "sanitation

effect" to refer to the culling of young, old or otherwise "inferior" animals of a prey population which contribute little to herd growth. Other studies, however, have shown that juvenile survival, in the absence of predation, can be high and are an important determinant of population growth (Bergerud 1978c, Gasaway et al. 1977, Ballard 1980). McCullough (1979) believed the culling effect is overemphasized since intraspecific competition within the prey population is probably capable of lowering reproductive success in genetically substandard deer. Also, substandard prey killed by wolves are usually inferior due to phenotypical causes (i.e., injuries, parasite loads, see Mech 1966, Mech and Frenzel 1971) and therefore are not a threat to the genetic quality of the deer.

Predation should stimulate prey productivity by lowering prey density and increasing food availability (Mech 1966). More recent studies (Peterson 1977, Mech and Karns 1977) have not shown increased reproductive rates from predation when habitat conditions are poor and winters severe. Keith (1974) and Connolly (1978) concluded that reproductive rates are related to nutritional conditions that can and do vary independently of predation rates.

Predators are hypothesized to keep ungulates moving on their winter ranges which helps to distribute browsing pressure more equitably (Leopold 1933, Hunter and Yeager 1956, Hornocker 1970).

Another influence of predation is that it may reduce behavioral plasticity by causing prey populations to be more uniform in their response to predators (Bergerud 1974). Bergerud suggested that this could conceivably reduce the ability of one species to respond to other environmental components.

5.2.3. Influences of Predation on Habitat Selection and Distribution of Ungulates

Habitat selection by ungulates can be a direct response to the need to hide or escape from predators while local changes in distribution can be related to attempts to avoid predation. This implies that the exploitation of plant

communities and the distribution of ungulates may be influenced as much by predation as habitat quality.

Hiding from predators is an important strategy of forest-dwelling species, both for young and adults (Lent 1974, Dasmann and Taber 1956, Sweeney et al. 1971). As well, most North American ungulates appear to use terrain to escape predation. Thus mule deer select broken terrain and steep long hillsides where their bounding gait gives them an energetic advantage over wolves, while white-tailed deer select creeks, swamps and open water to evade predators (Geist 1981). In summer, Woodland caribou use high ground on long open ridges where steep terrain provide good escape habitat while in winter they confine their movements to frozen lakes where they can outrun wolves (Geist et al. 1974, Bergerud and Butler 1978). In summer, moose stay close to shallow water, but in winter seek deep soft snow under conifer canopies to escape wolves (Geist et al. 1974). Both moose and caribou are known to calve on islands where predators are uncommon (Peterson 1955, Simkin 1965). Caribou also calve on high exposed ridges (Bergerud and Butler 1978). Mountain goats and mountain sheep utilize cliffs as escape terrain (Brandborg 1955, Murie 1944).

Ungulates will also alter their habitat use patterns to evade predators. Hornocker (1970) observed that mule deer and elk avoided areas where a mountain lion made a kill, often crossing to the far end of the watershed and in some instances left to enter a different drainage. Carbyn (1974) observed that regular visits to a salt lick by mountain goats was interrupted when a wolf pack established its rendezvous site at one of the licks. Ballard et al. (1980) and Franzmann and Peterson (1978) both showed that moose cows with calves disturbed by bears increased their home ranges. Corbett et al. (1971) found that white-tailed deer quickly left their home ranges to avoid dogs but returned in all cases if mortality had not occurred. However, black-tailed deer are reluctant to vacate their seasonal ranges (Geist 1981) and there is no indication that they leave their home ranges to avoid predators.

Nelson and Mech (1981) found that wolves affect the local distribution of deer in Minnesota. Wolves significantly reduce deer numbers in wolf pack territory cores but normally have little effect on deer living on the edges of wolf territories (Rogers et al. 1980). Hoskinson and Mech (1976) attributed this to greater survivability of deer in these areas rather than movements by deer to avoid wolves.

The foregoing indicates that predators could markedly influence habitat management practices. Peek (1980) suggested that wolves could prevent a sheep population response if range burned to enhance forage was not close to escape terrain. It is apparent that any attempts to enhance habitat in the territory centers of Minnesota wolf packs would show little if any deer response, although the same practice within buffer zones could show a dramatic response.

5.3 Predator-Prey Relationships on Vancouver Island

5.3.1 Wolf Ecology

5.3.1.1 Historical Records

The Vancouver Island wolf population has fluctuated considerably during this century with peaks occurring around 1910 and 1980. Annual reports of the Provincial Game Commission indicate wolves were very numerous from 1906 to 1910, but by 1925 the species was thought to be almost extinct. Reports from 1929 to 1938 stated a steadily increasing population, although numbers apparently did not expand to their previous level. Wolves declined from 1939 to 1942 and wolf sightings remained infrequent during the 1950's and early 1960's. Some recovery occurred by the late 1960's (Sumanik 1973). In 1970, the Vancouver Island wolf was included in the list "Endangered Wildlife in Canada" (Hebert 1981).

Evidence of a substantial increase in the 1970's is provided by the B.C. Fish and Wildlife Branch wolf sighting index. This suggests that wolves increased at 27% per year from 1976 to 1978 on the north end of the Island, which is close to the maximum rate of increase reported for wolves (Keith 1981). Possible reasons for population increases include recolonization from the northwest portion of the Island and immigration from

the mainland (Hebert 1981). Wolf densities during 1976-78 were greatest on the north end, and lowest on the south end. Presently, wolf numbers are stable or declining on the north end while increasing on the south end (Langin, pers. comm.)

5.3.1.2 Dynamics, Movements and Feeding Ecology

Scott (1979) estimated intrapack densities at one wolf/6.4 km^2 and one wolf/15 km^2 for two packs in the Adam watershed for the spring-fall period in 1978. Hebert et al. (1981) estimated the watershed density at one wolf/12km^2. Intrapack densities in 1981 declined by one-half but watershed densities appear only marginally lower despite a 40% reduction in the Adam deer population (Hatter in prep.). A noticeable reduction in wolf activity occured in the Nimpkish valley after deer numbers had declined by 75% (Jones and Mason, pers. comm.)

Pack sizes on the Island appear to be small (average = 6 to 7), probabably because of the small size of their primary prey, black-tailed deer. Fritts and Mech (1981) reported that pairs are more efficient at killing white-tailed deer than are packs. Pack sizes are expected to be larger on elk ranges (cf. Zimen 1976, Bowan 1981), but this hypothesis has not been adequately tested. Fritts and Mech (1981) reported that pairs are more efficient at killing white-tailed deer than are packs.

Wolf movements appear to be influenced by topography, roads, and prey density. Movements by pack members were greatest in early winter (Hatter in prep). Two lone wolves that were radio-tracked travelled extensively, often remaining in an area for 2-3 weeks before moving to a new locality. These observations are consistent with those reported on mainland populations (deVos 1950, Mech 1970, Mech and Frenzel 1971a, Mech 1977, Fritts and Mech 1981).

Scott and Shackleton (1980) reported that the major prey species in the Adam watershed is black-tailed deer, with elk and beaver used as secondary food sources. Deer fawns and elk calves are an important component of the summer diet. Hatter (in prep.) has shown that fawns are most prominent in the diet during June and July, but their use drops off in August. This was also supported by a concurrent fawn mortality study (see

5.3.2.1). The prevalence of juvenile cervids in the wolf's summer diet is well documented in the literature (see 5.2.1.1.2). Selection for deer over elk was reported by Carbyn (1974) as well.

5.3.1.3 Wolf Pack Territories and Prey Exploitation

Wolf research and general field observations on northern Vancouver Island suggest the following relationships between wolf pack territory occupancy and prey exploitation in a watershed:

(1) Wolves select high deer density areas when colonizing a watershed, often in close proximity to spring-summer elk concentrations (Mason, pers. comm.).

(2) Wolf pack territory size is inversely related to deer density while territory shape is dependent on topographic features (Hatter in prep.). Haber et al. (1976) showed that territory size is adjusted to maintain constant prey biomass. Thus with declining prey density, some packs can be expected to disappear while others will enlarge their territory.

(3) Winter territories are larger than summer territories (Hatter in prep.). This allows for territorial maintenance (Fritts and Mech 1981), and enables wolves to assess prey densities outside of summer territories.

(4) Territory shifts encompass areas of greater deer density. Areas previously heavily exploited receive little or no use (Mason, pers. comm.). This may allow some local recovery in the deer population.

(5) Predation pressure is localized within wolf territories and appears most intensive from April through September when wolves use den and rendezvous sites (Hatter in prep.).

(6) Predation pressure on deer is more severe in wolf territories with elk concentrations (Mason, pers. comm.; Hebert et al. 1981). This is probably because elk provide a source of alternate prey enabling wolves to continue exerting intense pressure on declining deer populations in elk occupied areas.

Predation could be more severe on resident than on migratory deer populations. Harestad (1979) hypothesized that wolves should concentrate their activities on spring deer ranges where prey density and foraging efficiency are greatest. Migratory deer have spatially segregated spring and summer ranges, but resident deer do not (Harestad 1979). Residents could be exposed to a higher risk of predation if wolves continue to exploit spring ranges through the summer. Wolves do exploit fawns more intensively near home sites (Hatter in prep.). Wolves probably also select their den sites on the basis of prey availablility during the denning period (April), which is when deer start to concentrate on spring ranges. Mason (pers. comm.) has noted that the most resilient deer herds in the Nimpkish are the migratory herds.

5.3.1.4 Habitat Selection

Den sites that have been investigated occurred in mature forest habitats. Rendezvous sites are known to occur in both forested and cutover habitats and are often near swamps (Scott 1979).

In the Adam River watershed, telemetry locations indicate wolves occupied valley bottom areas and only infrequently use sidehills or high elevation sites[1]. Wolves also avoided recent cutovers (0-5 years) but regularly used cutovers from 5-15 years of age. However, observation of wolves and their sign in the Nimpkish and Nanaimo River indicated that both sidehills and recent cutovers are used (Mason and Jones, pers. comm.; Davies, pers. comm.). Also, locations of wolf scats in the Adam during 1980 showed that wolves were using sidehills and high elevation sites in the Upper Adam. This suggests that wolves do not employ any overall habitat use strategy but hunt any habitats with high deer densities.

The influence of snow on wolf habitat selection and prey exploitation is not known. It is expected that wolves will concentrate their activities on ungulate winter ranges as reported by Mech and Karns (1977) and Fritts and Mech (1981).

[1] personal files of the author, Ministry of Environment, Fish and Wildlife Branch, Nanaimo, B.C.

Three scenerios are possible during a severe winter: (1) wolves will concentrate on ungulate winter ranges and kill deer in excess of their needs, as reported by Mech and Karns (1977) in Minnesota; (2) wolves will concentrate on winter ranges but resort primarily to scavenging winter kills as reported by Haber (1977) in Alaska; or (3) they may continue travelling throughout their winter territory and not take advantage of deer and elk concentrations, as reported by Carbyn (1974) in Jasper Park. Crusting increases hunting success for wolves (Peterson 1977). Crusts over deep snow will probably make elk particularly vulnerable by supporting wolves but interfering with elk movements. Snow-ungulate studies by Harestad and Bunnell (1979) may enable predictions on these interactions.

5.3.2 Effects and Influences of Wolves on Deer

5.3.2.1. Population Trends, Recruitment and Mortality

Black-tailed deer populations have declined at an annual rate of 24% where wolves are plentiful, 4-7% where wolf densities are light to moderate and increased at 13-22% where there are few or no wolves (Hatter 1982). Unsubstantiated reports indicate dramatic declines in deer populations on small coastal islands colonized by wolves (Mason, pers. comm.). Neither habitat nor climatic predisposing factors have been identified. In some instances, hunting has probably accelerated the declines.

Deer population trends have been directly related to summer wolf pack territories in the Adam River watershed. In 1978-79, deer numbers declined by 33% and 8% in the core home ranges of the Upper and Lower Adam packs respectively, but increased by 25% in the vacant wolf area between the two territories (Hebert et al. 1981). By 1980-81, the two territories partially overlapped and deer numbers now appear to be declining throughout the watershed (Hatter in prep.).

Low fawn survival seems to be the major factor limiting population growth (Hatter 1982, Jones and Mason 1982, Hatter in prep.). From 1977 to 1981, fawn recruitment averaged 31% in areas on the Island where wolves are few or absent, 24% in areas with light to moderate wolf densites and 9% in high wolf density

areas (Hatter 1982). Jones and Mason (1982) showed a highly significant correlation (r=.91) between fawn recruitment and wolf activity in the Nimpkish Valley. A fawn radio-telemetry study in the Adam watershed indicated wolves were the major mortality agent of fawns (Hatter in prep.). Predation was most intensive during the summer months and accounted for 8 of 14 mortalities in a sample of 28 radio-collared fawns. Fawns within a 3.2 km radius of den-sites appeared most vulnerable. Annual fawn survival was estimated at 27%.

Adult and yearling mortality has likely increased in watersheds with high densities of wolves. If McCullough's comments apply (see 5.2.1.1.2), there is probably little selection for older and substandard deer on Vancouver Island. The mean annual yearling and adult mortality rate in the Adam watershed for the period 1976-81 was roughly estimated at 30%. Recruitment averaged 23% for a 7% rate of decline (Hatter in prep.).

A computer simulation model of wolves and deer on Vancouver Island reflected the general behaviour of wolf-deer interactions studied to date and supports the predator-control hypothesis of population limitation in ungulates (Hatter in prep.).

5.2.2.2. Seasonal Movements and Habitat Selection

Presently, there is no direct information that wolves have influenced seasonal movements and habitat selection by deer. Jones and Mason (1982) found a close agreement between the reduction in pellet group (69%) and spotlight (59%) indices in the Nimpkish Valley from 1971 to 1979. This suggests wolves have not altered the nocturnal use of cutovers by deer. Hatter (in prep.) was also unable to show a habitat or movement response by radio-collared deer fawns that could be related to wolf activity. Jones and Mason (1982), however, believe that does hide their fawns more often when predator activity is high.

Casual observations indicate steep cliff areas provide escape terrain for deer and dense regenerating cutovers are used as hiding cover. Jones, Mason, and Smith (pers. comm.) believe a greater proportion of deer now use escape terrain but

it is not known whether this is a behavioural response (i.e. deer concentrating into these areas) or due to differential survival. It is also not known if deer are hiding more in dense cutovers.

Harestad (1979) hypothesized that the movement of deer from spring home ranges onto the larger summer home ranges is influenced by predation.

5.3.3. Effects and Influences of Wolves on Elk

5.3.3.1 Population Trends, Recruitment and Mortality

The impact of wolf predation on elk is still poorly documented. A wolf scat analysis in the Adam watershed indicated wolves use elk as an alternate prey in winter, and that calves comprise the main component of the summer diet (Scott and Shackleton 1980). However, the proportion of adult and calf elk in the diet is inconsistent with elk distribution data (Hebert et al. 1981). Another scat analysis in the Sayward Forest indicated elk comprised the major portion of the wolves diet (Becker 1982). Thus the importance of elk in the wolf diet probably varies between packs, dependent on elk availability.

Age ratio data suggest that productivity and survival of elk reflect the influence of extensive timber harvesting and winter weather, rather than wolf predation (Hebert et al. 1981). However, recent surveys indicate calf/cow ratios are starting to decline on northern Vancouver Island, (e.g., surveys in the Nimpkish watershed show substantial declines in calf/cow and % yearling ratios [D. Janz, pers. comm.]). As the north Island and particularly the Nimpkish have the highest wolf densities and most suppressed deer population, wolves may have increased their utilization of elk as an alternate prey item. It was also conjectured earlier (5.3.1.4) that snow would increase elk vulnerability allowing increased predation pressure at this time.

5.3.3.2 Seasonal Movements and Habitat Selection

Janz (pers. comm.) believes that increases in elk group size and shifts in distribution have occurred coincident with increasing wolf populations. Elk also appear to be avoiding

natural openings more, suggesting more use of hiding cover. At present, this information is inconclusive since group sizes may be a response to other factors (e.g., increased elk density), and distribution shifts require more investigation. Nevertheless, the potential impact of wolf predation on elk habitat selection appears to be high. Their contagious distribution, gregarious nature, larger home ranges and use of descrete calving grounds would imply they are more susceptible to predatory influences than are deer.

5.3.4 Effects and Influences of Cougars on Deer and Elk

Deer are the major prey species of cougars, although beaver (Dewar and Dewar 1973) and elk (Janz and Lloyd 1977) are also eaten. Dewar and Dewar (1973) reported that cougars did not select for age, sex or condition in adult deer, whereas Cowan (1956) reported that Island cougars killed mainly bucks. Other investigators have also concluded that cougars kill more bucks than does (Robinette et al. 1959, Hornocker 1970, Spalding and Lesowski 1971, Shaw 1977). These authors attributed this to the tendency of bucks to frequent higher elevations or broken terrain that are also the preferred habitat of mountain lions. Vancouver Island cougars probably select fawns during the summer months, as shown in other studies (Robinette et al. 1959, Nellis 1977).

The effect of cougar predation on deer numbers received some investigation at Northwest Bay, Vancouver Island. Smith (1968) concluded that seral succession was the indirect cause of the deer decline from 1954-1966, but annual population levels were dependent primarily upon winter weather and hunting. The density of cougars was estimated at one cougar/26-65 km^2 (Christensen and Fisher 1976; Davies, pers. comm). Given a pre-hunt population of 4000 deer on the 350 km^2 study area (Smith 1968) and a kill rate of 1 deer/cougar/week during winter (Robinette 1959) cougars could have removed 5%-12% of the fall deer population. Hunting removed about 15% (Smith 1968). Although the above calculations are admittedly rough, they do support the contentions of Nellis (1977) and Shaw (1977) that cougar predation and hunting can limit deer populations.

The effect of cougar predation on elk is not known. Cougars probably select deer over elk and it is doubtful that cougars would adversely affect elk numbers unless severe declines in the deer population occurred first.

The influence of cougars to distribute deer on winter ranges (Hornocker 1970), was reported by Dewar and Dewar (1975) for Northwest Bay, although they provided little evidence for this statement.

5.3.5 Effects and Influences of Black Bear on Deer and and Elk

Black bear predation appears to be restricted to neonates. Hatter (in prep) working in the Adam River watershed found that 9% of 221 summer bear scats contained deer hair mostly from fawns. This compares favourably with 12% in California (Longhurst et al. 1952) and 8% in Washington (Schwartz and Mitchell 1945). Eighty-five percent of the fawn occurrences were in June scats. Only one out of 28 radio collared fawns (4%) was killed by a black bear. This supports the contentions that bear predation is restricted primarily to fawns during June, and that it has little impact on fawn survival.

Bear predation on elk calves may be more serious than on deer fawns. In Idaho, Schlegel (1976) reported that the total mortality of calf elk from calving through October was 68%. Predation, primarily by black bear, was responsible for 94% of this mortality.

Bears apparently learn to prey on juvenile cervids, and those species that predictably concentrate on discrete calving grounds (e.g., moose, caribou, elk) are the ones most susceptible to bear predation (Bergerud and Butler 1978, Franzmann et al. 1980, Ballard et al. 1981). Individual bears may become habitual fawn killers (Cowan 1956). Mason (pers. comm.) had a case reported to him on Vancouver Island in which a bear was caching fawns in the timber.

The potential for habitat manipulation to alter bear-ungulate interactions in favour of the prey was demonstrated on the Kenai Peninsula, Alaska (Swartz and Franzmann, 1980). Black bear predation on neonatal moose calves was significantly

reduced by mechanical crushing of the standing vegetation. Bears avoided the crushed areas which in turn also improved the habitat for moose by increasing the quantity and diversity of woody browse.

6 UNKNOWNS AND SPECIFIC PROBLEMS IN SECOND-GROWTH FORESTS

Much remains to be learned about predator-prey relationships in coastal forests. Predation studies on Vancouver Island have been confined to mature forest-early regeneration systems. These have largely been concerned with the effects of wolf predation; little is known about the influences of predators, and much less is known about the predators themselves. Predator-prey studies in second growth forests are nonexistent. Below is a list of specific questions regarding predation and predator ecology in second growth forests.

6.1 Predation Effects and Influence on Ungulates

6.1.1. Effects on Deer and Elk Populations

(a) The effects of predators, particularly wolves, on recruitment and survival of deer and elk. Does this vary between resident and non-resident herds? (see 5.3.1.3)

(b) The influence of environmental heterogeneity on predator impact. Do isolated blocks of mature timber concentrate deer and elk and increase their vulnerability to predation? Intensive silviculture in the future will increase heterogeneity in forest stands (Nyberg, pers. comm.). Will this also improve the opportunities for wolves to locate deer and elk (cf. Bergerud 1981)?

(c) The potential of silvicultural practices to alter predator impact. What is the capability of escape and hiding cover to limit the functional response of predators? How can the important physical characteristics of hiding and escape cover be measured and therefore be incorporated into silvicultural practices?

(d) The influence of snow to alter predator-prey relationships. Under what snow conditions and in what habitat types do deer and elk have the best and least chances for escape from predators?

(e) How significant is bear predation on elk calf survival?

6.1.2. Influences on Deer and Elk Populations

(a) The capability of predators, particularly wolves, to influence deer and elk habitat selection and movement patterns. If predators cause deer and elk to select for hiding and/or escape cover over nutritional quality, how should the spatial distribution of cover be apportioned to feeding sites to ensure that silvicultural practices that increase forage quality are accessible to deer and elk?

6.2 Predator Ecology

(a) The densities of predator populations. What are the factors limiting their size?

(b) The factors influencing where, when and how predators hunt. What are the important cues that predators use to select hunting sites? (i.e., prey density, cover type and density, topography, roads). At what time of day do they hunt? What strategies do they employ to capture prey?

(c) The diet and prey selection of wolves, cougars, and black bears. How do these vary under different deer: elk availability ratios?

(d) What are the ecological conditions which initiate predator (wolf and cougar) switching between deer and elk?

(e) The interspecific relationships between wolves, cougars and black bears. Does competition or mutual avoidance between wolves and cougars reduce the effect of predation on deer?

6.3 Confounding Potential of Wolf Predation on Deer/Elk Research Projects

The current IWIFR research program on deer and elk in second growth forests is investigating habitat utilization, animal condition, and population statistics as indicators of ungulate responses to habitat changes.

Some hypothetical relationships demonstrating the confounding potential of wolf predation to mask population and habitat use responses are outlined below:

(1) Wolf numbers respond rapidly to changes in deer density but social constraints on the wolf population limits further growth at higher deer densities (Fig. 3a).

(2) A net annual increment or recruitment curve for deer in the presence of wolves has a large "predator pit" which encompasses most of the observed range of deer densities on the Island (Fig. 3b).

(3) The effects of wolf predation on summer fawn survival is most severe near den sites (Fig. 3c).

(4) Wolves show little aggregative response to areas with low deer densities but respond strongly to a range of deer densities. They do not, however, distinguish between different areas of high deer density (Fig. 3d).

(5) Deer are preferred over elk in the wolves diet. However, as the elk:deer ratio increases, utilization of elk increases disproportionately (Fig. 3e).

(6) Increased wolf activity increases summer movements and therefore home range sizes of elk calf:cow groups (Fig. 3f).

(7) During April and May, the concentration of deer on spring ranges increases the risk of predation. Where predation is severe, fitness is increased through bypassing spring ranges and migrating directly from winter onto summer home ranges where the "spacing out" effect reduces predation risk (Harestad 1979, Fig. 3g).

(8) Elk show little selection for closed habitats (i.e. forested and conifer seral stages) under low wolf densities but respond strongly at higher densities (Fig. 3h).

(9) The probability of a successful attack, as a function of the initial wolf-deer distance, is dependent on topography with success highest on flat terrain (Fig. 3i).

(10) The probability of a successful attack, as a function of the initial wolf-deer distance, is also dependent on cover

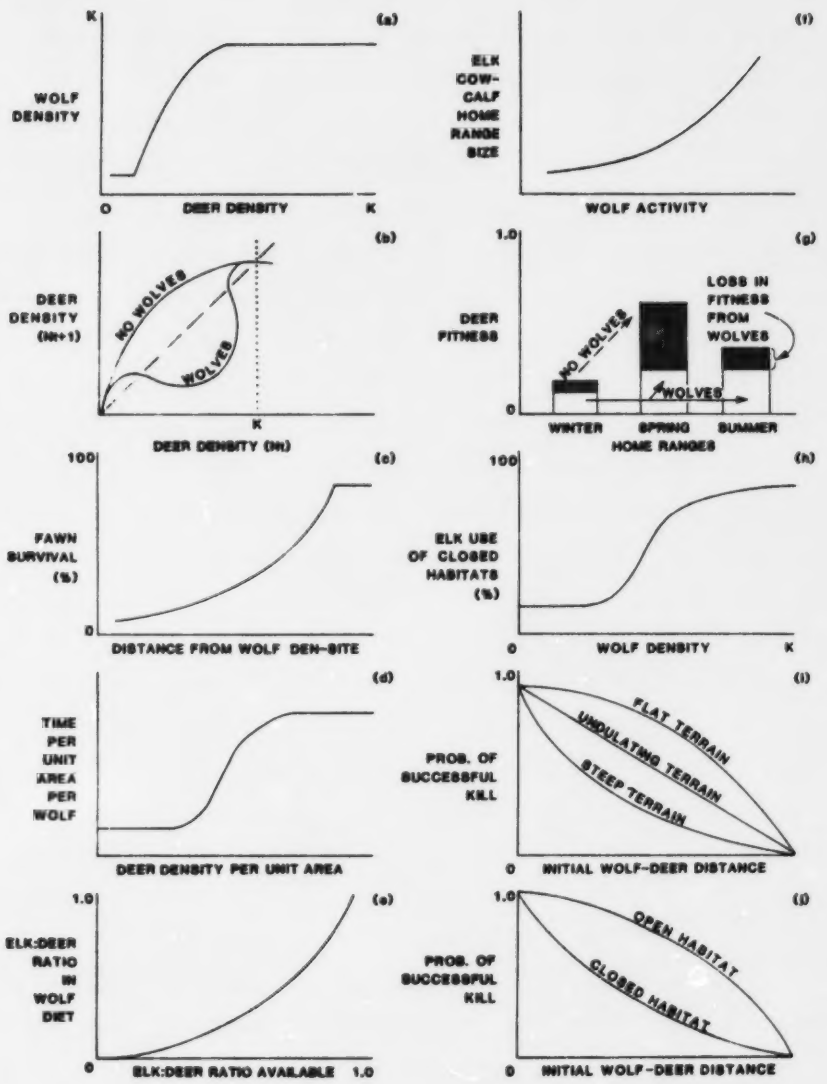

Figure 3. Hypothetical relationships demonstrating the confounding potential of predation on the IWIFR deer and elk research program (a) numerical response of wolves to deer density, (b) net annual increment or recruitment curve for deer in the presence of wolves, (c) effect of den site location on summer fawn survival, (d) aggregative response of wolves to deer density, (e) percent of elk in wolf diet, (f) influence of wolf activity on summer elk cow-calf home ranges, (g) influence of predation on seasonal movements of deer, (h) influence of wolves on elk use of closed habitats, (i) relationship of topography to attack success for deer and (j) relationship of cover to wolf attack success for deer.

(i.e. stand density). Success is highest in open habitats (Fig. 3j).

Based on the foregoing, the potential of wolves to confound interpretation of research findings is high (Table 1). Deer studies will be mainly affected through high mortality and elk studies through changes in habitat selection and movements.

Table 1. Potential of wolves to confound the interpretation of IWIFR findings for deer and elk

Factor	Magnitude of Impact	
	Elk	Deer
Population dynamics		
Juvenile recruitment	Moderate	High
Adult mortality	Low	Moderate
Dispersion	Moderate	Low
Habitat selection	High	Moderate
Local movements	High	Moderate
Animal condition	Low	Low

7 RECOMMENDATIONS

Until more information is available, integration of wolf management into ungulate-habitat systems can only be effected through reducing wolf numbers. The long-term management objective should be to mitigate wolf-ungulate interactions in favour of deer and elk. If this can not be done through habitat management, maintenance of wolf densities at a level compatible with ungulate management objectives will be necessary.

With respect to the IWIFR program, research emphasis should be directed towards the potential influence of predation on ungulate habitat selection, and the capability of habitat manipulations to alter wolf-ungulate interactions. It is recommended that an experimental wolf control program and a wolf radio-telemetry study be incorporated into the IWIFR program. Wolf, deer, and elk studies should be integrated as a systems research project. Both baseline and intensive investigations should be conducted.

7.1 Baseline Investigations

Baseline investigations should be initiated on all IWIFR second growth study areas to identify potential predatory effects and influences. Table 2 lists the study topics and proposed methodologies. These studies should be implemented by the deer and elk research biologists. Results from these studies can be used to select an intensive study area for integrated wolf-ungulate-habitat studies as well as provide baseline ecological data on predator-prey relationships for future hypothesis testing. If predatory effects appear severe on other study areas, wolf numbers may have to be reduced.

7.2 Intensive Investigations

The most suitable method for documenting wolf predation effects and influences is to compare ungulate responses in an area with wolves (control area) to one where wolf numbers have been reduced (removal area) and in which all other ecological conditions are similar (Mech 1970).

It is recommended that this approach be adopted for intensive investigations. Deer and elk research studies should be conducted in both the control and removal area. Results will

Table 2. Study topics for baseline predator-prey investigations

	Objective	Proposed Methodology	References
a)	**Predation Effects**		
1.	population trends of deer and elk.	-spotlight counts and aerial surveys, relate to predator abundance (see below)	Jones and Mason 1982
2.	recruitment and mortality rates of deer and elk.	-identify areas of high/ low fawn-doe and calf: cow ratios and spring carryover, relate to predator abundance (see below)	Jones and Mason 1982 Janz 1980
		-mortality rates and causes of mortality in radio-collared deer and elk.	Hauge and Keith 1981
b)	**Predator Ecology**		
1.	the distribution and relative abundance of wolves, cougars, and black bears.	-mapping of predator sightings, tracks, scrapes and scats.	Youds and Brunt (pers. comm.)
		-wolf scat transects	Hatter in prep.
2.	seasonal food habits of wolves, cougars, and black bears.	-scat collection and analysis.	Carbyn and Kingsley 1979, Hornocker 1970, Hatler 1972.

be most causative when the control and removal areas coincide with wolf pack territories. This is because wolf predation effects are most accurately measured on a wolf pack territory-to-territory basis and elimination of whole packs, rather than parts of many packs, appears to be the most effective removal technique (Haber et al. 1976, Haber 1978). This necessitates that wolves are radio-collared and pack territories delineated in both areas prior to reducing wolves in the removal area.

Table 3 lists the study topics for an intensive investigation. A separate predator research team will be required to initiate these studies.

7.2.1 Study Areas

Selection of the control and removal areas should satisfy the following requirements:

1. The control and removal areas are each large enough to encompass the winter territory of at least one wolf pack, as well as the movements of radio-collared deer and elk. A buffer zone, preferably the territory of another wolf pack, is present between the control and removal areas. The study area should therefore include at least 3 wolf pack territories. It would be preferable to use one watershed as a control and another as the removal area.
2. Both the control and removal area must be easily assessible with an extensive road network for monitoring.
3. A similar wolf effect (comparable rates of decline and recruitment for deer and elk) are present in both areas.
4. Habitat and topographic features are similar in both areas.
5. Deer numbers in the control and removal areas are high enough for statistical analysis of spotlight and classification counts.
6. A minimum of 5 years of deer population trend and composition data is available for both areas.

Table 3. Study topics for intensive predator-prey investigations

	Objective	Proposed Methodology	References
a)	Wolf Reduction		
1.	75-90% reduction of wolves in removal area.	-trapping and shooting of wolves in removal area. -wolf scat transects to monitor wolf activity in control and removal areas.	Scott 1979 Hatter in prep
b)	Predation Influences		
1.	influence of wolves on deer and elk habitat selection and movement patterns.	-contrast radio-collared deer/elk movements, home range sizes, and habitat selection in control and removal areas. -analyze linear movements data between radio-collared wolves, deer, and elk.	Ballard et al. 1980
2.	influence of wolves on seasonal and nocturnal use of cutovers by deer.	-contrast timing, duration, and variability of spring and summer use of cutovers in the control and removal areas.	Harestad and Jones 1981
3.	the physical characteristics of security (hiding and escape) cover and quality of security cover in different habitat types.	-contrast habitat types used by radio-collared deer and elk control and removal areas. -visual observations and interpretation of tracks in snow of wolves pursuing deer and elk.	Hoskinson and Mech 1976, Nelson and Mech 1981
c)	Predation Effects		
1.	deer population trends in control and removal areas.	-spotlight counts.	Harestad and Jones 1981
2.	recruitment and mortality rates of deer and elk in control and removal areas.	-fawn:doe, calf:cow ratios in August, % carryover in spring. -mortality rates and causes of mortality in radio-collared resident and migratory deer and elk.	Jones and Mason 1982, Janz 1980 Hauge and Keith 1981
3.	effects of wolves on deer in small isolated blocks of mature winter range.	-occurrence of wolf radio-telemetry locations in the vicinity of small, isolated winter ranges.	Fritts and Mech 1981

4.	effects of snow conditions on the vulnerability of deer and elk to wolf predation in different habitat types.	-foot loadings of wolves, deer and elk in different habitat types (i.e. different snow depths and density).	Mech and Frenzel 1971
5.	evaluation of escape cover in reducing wolf functional response.	-snow tracking to document successful vs. unsuccessful prey capture attempts in different habitat types.	Kolenoksy 1972
6.	effects of wolves on beaver populations.	-wolf scat analysis. -inventory of beaver colony sites in wolf-occupied and wolf-free areas.	Hall 1971
d)	Predator Ecology		
1.	wolf densities, pack sizes and spatial relationships.	-direct enumeration and radiotelemetry of wolves in control and buffer areas.	Fritts and Mech 1981
2.	habitat use by wolves.	-radiotelemetry of wolves in control area for analysis of preference/availability of habitat types.	Andelt 1981, Neu et al. 1974.
3.	seasonal food habits of wolves in areas with different deer-elk availability ratios.	-scat analyses in primarily elk occupied vs. deer occupied areas, in severe vs. mild winters.	Carbyn and Kingsley 1981
4.	recruitment, mortality and population trends of wolves.	-direct observations of percentage of pups. -mortality rates of radio-collared wolves. -changes in pack sizes and number of packs in control and buffer areas.	Mech 1977
5.	evaluation of wolf inventory techniques in coastal forests.	-correlation of wolf howling surveys, scat transects and the wolf sighting index to known wolf densities.	Theberge and Strickland 1978, Hatter, in prep., Hebert et al. 1981

7. Deer and elk densities are similar in both areas.

7.2.2 An Alternate Proposal

At present there is not an IWIFR site that can satisfy all the requirements for a study area. Most of the deer study sites are too small to establish control and removal areas. Elk studies have been established in the Sayward Forest but only limited deer research is anticipated here (Davies, pers. comm.). Thus it may be necessary to utilize several study areas to address the various study topics outlined in Table 3. An alternate proposal, that should be feasible, is outlined below:

1. Control wolves on IWIFR study areas where wolf effects appear significant (e.g. Nanaimo River).
2. Select one IWIFR study area (e.g. Sayward Forest) and radio-collar wolves to measure predation influences on elk and deer. Related aspects of wolf ecology and predator-prey relationships can also be studied.
3. Initiate the Nimpkish deer/wolf study, an experimental wolf control project, to study the cost-effectivess of wolf control in a depressed deer population (Langin 1982).

The alternate proposal should reduce the confounding potential of excessive wolf predation on second growth ungulate studies. The influence of wolves on deer and elk habitat selection and the effect of different habitats in reducing predation risk will be investigated. The cost-effectiveness of wolf control can also be ascertained. This, in conjunction with continuing wolf telemetry studies in the Adam River, should provide a good foundation for integrating predator-ungulate systems into intensive forestry management.

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